Genetic mapping of quantitative trait loci affecting body weight, egg character and egg production in F2 intercross chickens

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Summary

Phenotypic measurements of chicken egg character and production traits are restricted to mature females only. Marker assisted selection of immature chickens using quantitative trait loci (QTL) has the potential to accelerate the genetic improvement of these traits in the chicken population. The QTL for 12 traits (i.e. body weight (BW), six for egg character, three for egg shell colour and two for egg production) of chickens were identified. An F2 population comprising 265 female chickens obtained by crossing White Leghorn and Rhode Island Red breeds and genotyped for 123 microsatellite markers was used for detecting QTL. Ninety-six markers were mapped on 25 autosomal linkage groups, and 13 markers were mapped on one Z chromosomal linkage group. Eight previous unmapped markers were assigned to their respective chromosomes in this study. Significant QTL were detected for BW on chromosomes 4 and 27, egg weight on chromosome 4, the short length of egg on chromosome 4, and redness of egg shell colour (using the $L*a*b*$ colour system) on chromosome 11. A significant QTL on the Z chromosome was linked with age at first egg. Significant QTL could account for 6–19% of the phenotypic variance in the F2 population.

Keywords egg character, egg layer, egg production, quantitative trait loci.

Introduction

Marker assisted selection (MAS) using quantitative trait loci (QTL) has the potential to enhance the accuracy of selection in animal breeding programmes, particularly for the traits that are difficult to improve through traditional selection methods (Meuwissen & Goddard 1996; van der Beek & van Arendonk 1996). In chickens, the current method for estimating the breeding values of egg character and production trait is not particularly accurate in immature females and males. The data of the chickens for selection and their sib (full and half) cannot be used when chickens are selected at immature ages for egg character, because the measurements of egg character and production trait are restricted to mature females only. In this

case, the estimated breeding value of a particular chicken is the average of its parents' additive genetic effects. The breeding value of the chickens for selection cannot consider the Mendelian sampling effect. Therefore, the accuracy of the estimated breeding value of an immature chicken is limited even if the data of relatives are used for estimation of breeding values. The expected genetic progress may be small when the animals are selected at immature ages. The genetic gain is proportional to the reliability of selection, which is low in this case. Thus, a better understanding of chicken QTL may facilitate accurate selection of immature chickens. Therefore, MAS of immature females and males should greatly enhance genetic progress for egg character and production traits through accurate selection and accelerate genetic improvement via selection at a young age.

Several studies have reported poultry QTL for body weight (BW) and feed efficiency (van Kaam *et al.* 1998, 1999; Tatsuda *et al.* 2000; Tatsuda & Fujinaka 2001) as well as egg character and production (Tsuiskula-Haavisto *et al.* 2002; Wardecka *et al.* 2002, 2003; Kerje *et al.* 2003).

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However, these studies focused on specific areas of the chicken genome. Further studies are warranted to identify additional useful QTL for the enhancement of egg character and production trait.

Egg shell strength (ESS) is one of the important quality traits in a layer breed, as broken and cracked eggshells lead to major economic losses for egg producers (Hamilton *et al.* 1979). Egg shell colour is additionally important in some markets (Hunton 1962). For example, brown shell eggs fetch a higher price in the Japanese market. However, limited data are currently available on QTL for these traits (Tsuiskula-Haavisto *et al.* 2002; Wardecka *et al.* 2002, 2003).

The aim of this study was to detect QTL for BW, egg character (including ESS and shell colour) and production traits, and estimate their effect on phenotypic variance using a resource family produced by crossing White Leghorn (WL) and Rhode Island Red (RIR) breeds.

Materials and methods

The F2 population originated from a cross between WL males and RIR females (P; parents generation). The parental WL line was developed at the National Institute of Livestock and Grassland Science. The WL line was selected for reduction in non-destructive deformation of eggs for 14 generations (Nirasawa *et al.* 1998), and thereafter maintained without selection. In order to find QTL regarding ESS, the 18th generation of this line was used for our experiments. The parental RIR chickens were fed at the Okazaki Station of National Livestock Breeding Center. F1 chickens were produced by crossing five WL males with 16 RIR females, with one to four females randomly selected to mate with each male. Two hundred and sixty-five F2 females were produced by crossing 16 F1 males with 60 F1 females, with one to five full-sib females randomly selected to mate with each male. The F2 chickens were hatched on the same day in the same incubator. These animals were raised in the same chicken house and fed the same food for the duration of the experiment. Experiments were performed according to the guidelines for the care and use of agricultural animals in agricultural research and teaching.

Body weight was measured at 239 days of age. Six egg characters were measured, including egg weight (EW), short length of egg (SLE), long length of egg (LLE), ESS, egg shell thickness (EST) and egg shell weight (ESW). Egg shell colour was measured on a Colorimter 300B (Nippon Denshoku, Tokyo, Japan) using the $L^*a^*b^*$ colour system, in which the L^* (lightness) value is a luminance or lightness component, the a^* (redness) value is a chromatic component from green to red and the b^* (yellowness) value is the chromatic component from blue to yellow. For each individual, egg characters and shell colours were measured for the first three eggs (245–251 days of age). Egg production ratio (EPR) was defined as the number of eggs divided by the number of producing days from 169 to 280 days, and the age at first egg (AFE) was also measured as an egg production trait.

Blood samples were collected from 21 parents of F1 and 265 F2 chickens. Genomic DNA was extracted from whole blood using the Easy-DNA Kit (Invitrogen Corporation, Carlsbad, CA, USA). GeneScan 3.1.2 and Genotyper 2.5 software (Applied Biosystems Japan, Tokyo, Japan) were employed to determine the alleles. A total of 498 primer sets were used with Microsatellite Kits 1–2, 3 and 4 (US Poultry Genome Project 2001).

Linkage and QTL analyse were performed using the program Map Manager QTX b18 (QTX) (Manly & Cudmore 2001). Linkage groups were determined using the 'Marker Linkage Groups' command of QTX with Kosambi map function by $P = 0.0001$ search linkage criterion. The QTL mapping was determined with the 'Interval Mapping' command of QTX, which is based on the work of Haley & Knott (1992), Martinez & Curnow (1992) and Zeng (1993, 1994). The additive effect of RIR QTL alleles is half the phenotypic difference between birds carrying two RIR alleles and those carrying two WL alleles.

Linkage analysis and QTL mapping of the Z chromosome cannot utilize the F2 intercross type cross option. Instead, F2 intercross data were converted into back cross data for analysis of the Z chromosome (Yasukouchi 1998).

The chromosome-wide critical threshold levels for significant QTL were determined by 10 000 permutation tests for each trait using the 'Permutation Test' command of QTX, which estimates an empirical chromosome-wide probability for observing a given likelihood ratio statistic (LRS) score by chance (Churchill & Doerge 1994). The *P*-value was calculated by interpreting the LRS as a χ^2 statistic. The genome-wide critical threshold value was derived from the chromosome-wide critical threshold by application of the following Bonferroni correction:

$$P_{genome-wide} = 1 - (1 - P_{chromosome-wide})^{1/r}.$$

The *r*-value was obtained by dividing the length of the chromosome by the total analysed genome length (Tsuiskula-Haavisto *et al.* 2002).

Results

Trait data are presented as mean values and standard deviations in Table 1.

A total of 498 markers were initially tested for their information contents in the WL and RIR breeds. Markers at which the P breeds shared alleles could not be used in the analysis, as the origin of these alleles in the F2 generation could not be determined. A total of 123 informative markers were found to be informative, and were subsequently used to genotype all 21 P and 265 F2 chickens. Of these, 96 markers were mapped into 25 linkage groups on 18 autosomes (chromosomes 1–11, 13–15, 17 and 26–28) and one autosomal linkage group (E47W24) (Fig. 1). Chromosome 1

Table 1 Phenotypic values of quantitative traits.

	Number	Minimum	Maximum	Mean	SD
BW (g)	262	755	2980	1878	310
EW (g)	244	41.75	73.71	55.12	4.92
SLE (cm)	244	39	47.67	43	1
LLE (cm)	244	49	62	55	2
ESS (kg)	243	1.46	4.94	3.19	0.56
EST (μm)	244	208	379	303	27
ESW (g)	244	2.94	6.25	4.73	0.50
Lightness	244	58.84	95.47	84.42	5.34
Redness	244	1.08	17.47	8.73	3.51
Yellowness	244	6.24	34.67	21.19	5.72
EPR (%)	258	1.8	97.3	80.4	17.9
AFE (day)	258	123.0	205.0	146.5	13.4

BW, body weight at 239 days of age; EW, egg weight; SLE, short length of egg; LLE, long length of egg; ESS, egg shell strength; EST, egg shell thickness; ESW, egg shell weight; Lightness, luminance or lightness component; Redness, chromatic component from green to red; Yellowness, chromatic component from blue to yellow; EPR, egg production ratio (169–280 days of age); AFE, age at first egg.

was separated into four linkage groups (chromosome 1a, 1b, 1c and 1d), chromosome 2 into three linkage groups (chromosome 2a, 2b and 2c) and chromosome 5 into two linkage groups (chromosome 5a and 5b). Our linkage groups encompassed 800 cM of the autosomes based on the Kosambi mapping function. Thirteen markers were mapped into a linkage group on the Z chromosome, encompassing 120 cM of the Z chromosome. The total linkage map spanned 920 cM, with an average marker spacing for 6.7 cM. The remaining 13 markers could not be assigned to a linkage group and were therefore excluded from the QTL analysis.

Almost all of the linked markers were assigned in the same order as reported previously (Groenen *et al.* 2000; ArkDB URL 2001; US Poultry Genome Project 2001; Lee *et al.* 2002), and we assigned eight previously unmapped markers to their respective chromosomes in this study: six autosomal markers (*MCW0215* and *MCW0298* on chromosome 2, *MCW0171* and *LEI0125* on chromosome 4, *LMU006* on chromosome 9, *MCW0105* on chromosome 14, *MCW0012* on chromosome 27 and *MCW0227* on chromosome 28) and two on the Z chromosome (*MCW0237* and *LEI0123*).

Suggestive LRS thresholds ($P < 0.10$) in a genome-wide scan of the QTL position of each trait were 8.5–8.7 for the autosomes and 6.0–6.2 for the Z chromosome. Significant LRS thresholds ($P < 0.05$) in a genome-wide scan of the QTL position of each trait were 14.9–15.2 for the autosomes and 11.9–12.1 for the Z chromosome, and highly significant LRS thresholds ($P < 0.01$) were 22.2–24.4 for the autosomes and 18.7–20.8 for the Z chromosome. The variations in threshold levels between the autosomes and Z chromosome were caused by differences in the degrees of freedom of the analytical method employed.

Six genome-wide significant QTL effects were identified for two BW, two egg character, one egg colour and one egg production traits (Table 2). One highly significant QTL associated with BW was located between *MCW0122* and *LEI0062* on chromosome 4. Another QTL significantly linked with BW was located on *ADL0376* of chromosome 27. The peak LRS score was on *ADL0376* and therefore the real peak may be beyond *ADL0376*. These QTL on chromosomes 4 and 27 account for about 17 and 6% of the total phenotypic variation of BW, respectively. On chromosome 4, one highly significant QTL associated with EW was located between *LEI0081* and *MCW0122*. Another highly significant QTL associated with SLE was assigned to similar position on chromosome 4. These QTL for EW and SLE accounted for about 17 and 16% of the total phenotypic variation, respectively. One QTL significantly linked with redness was identified between *LEI0072* and *LEI0214* on chromosome 11, accounted for about 19% of the total phenotypic variation. A QTL significantly linked with AFD was located between *ADL0201* and *MCW0241* on the Z chromosome and explained about 6% of the total phenotypic variation.

Twenty-one genome-wide suggestive QTL effects were identified for two BW, 13 egg character, one egg production and five egg colour traits (Table 2). These QTL were located on chromosomes 1a, 1b, 4, 5a, 6, 7, 9, 11, 17 and Z, and accounted for between 2 and 13% of the total phenotypic variation.

Discussion

A significant QTL for BW was identified on chromosome 4 in this study. Significant QTL for BW at 6 and 9 weeks were reported at similar positions on this chromosome from an intercross line between commercial broiler and WL (Sewalem *et al.* 2002). A significant QTL for BW was reported at similar position on this chromosome from an intercross between WL and RIR (Tsuiskula-Haavisto *et al.* 2002). The additive and dominance effects of the QTL in the previous study are consistent with our results and may represent the same locus, as the same original breeds were used in both studies. We identified another significant QTL for BW on chromosome 27, which has already been reported (Sewalem *et al.* 2002; Kerje *et al.* 2003). The positions of the previously reported QTL were close to those determined in this study.

The number of informative markers was limited in this study because the typing of the F1 generation was not possible. Therefore, the genome was not fully covered and the marker spacing was not uniform. However, the size of F2 population, the marker number and spacing were sufficient for reliable QTL detection.

Numerous studies demonstrate that QTL displaying significant linkage with BW and located on chromosome 1 (Groenen *et al.* 1997; Tatsuda *et al.* 2000; Tatsuda &
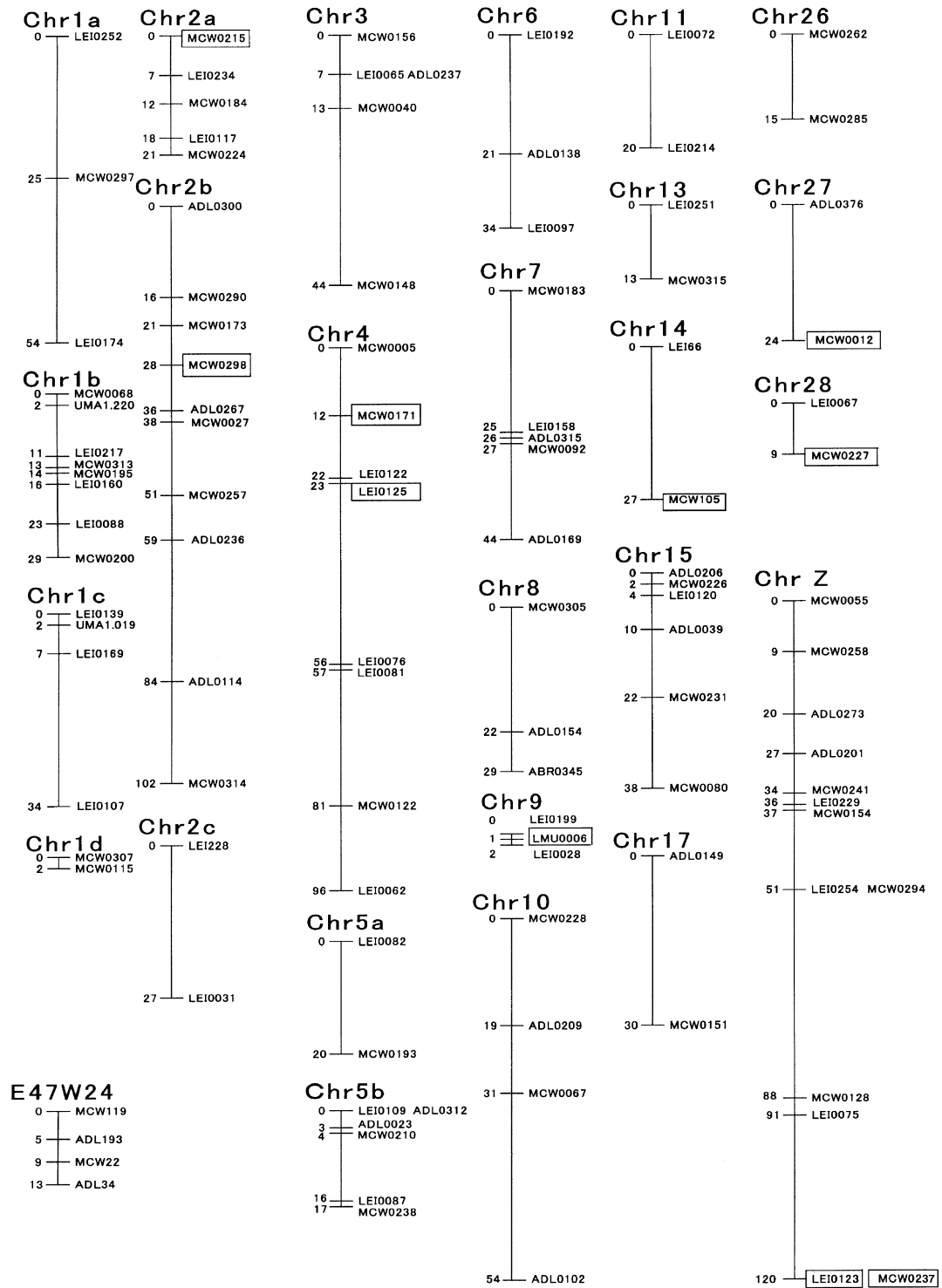
Figure 1 Linkage map for quantitative trait loci analysis, including positions and names of the markers. In this study, the enclosed markers are located at positions based on the Kosambi mapping function. Twenty-four linkage groups were identified on 18 autosomes (Chr 1–11, 13–15, 17, 26–28). Linkage groups on chromosome 1 were separated into four groups (Chr 1a, 1b, 1c, 1d), chromosome 2 into three groups (Chr 2a, 2b, 2c), and chromosome 5 into two groups (Chr 5a, 5b). One linkage group was located on the autosomal E47W24. Another linkage group was located on the Z chromosome (Chr Z). The boxes denote the positions of previously unmapped markers.

Table 2 Summary of genome-wide suggestive and significant quantitative trait loci (QTL) for body weight, egg character, egg shell colour and egg production traits.

Trait	Chromosome	LRS	Flanking markers	Position[1](cM)	a[2]	d[3]	Variance explained (%)
BW	4	46.3**	MCW0122-LEI0062	88	193.84	−21.96	17
	17	9.4[†]	MCW0151	30	45.27	90.66	4
	27	16.3*	ADL0376	0	100.37	16.18	6
	Z	8.3[†]	LEI0075-LEI0123	96	120.08	–	3
EW	4	45.8**	LEI0081-MCW0122	76	3.01	−0.60	17
	5a	10.2[†]	LEI0082	0	−0.05	2.11	5
	9	7.3[†]	LMU0006	1	−1.13	−0.59	3
SLE	4	41.9**	LEI0081-MCW0122	75	0.83	0.04	16
LLE	4	12.2[†]	MCW0122	81	0.54	−0.53	5
	7	10.2[†]	MCW0183-LEI0158	15	−0.14	−1.16	4
ESS	1b	12.4[†]	MCW0200	29	−0.01	0.25	5
	4	9.8[†]	LEI0125-LEI0076	36	−0.01	0.35	4
	7	9.8[†]	MCW0183-LEI0158	16	0.19	0.00	4
	Z	8.0[†]	MCW0154-LEI0254	47	0.21	–	3
EST	1b	11.9[†]	MCW0200	29	0.61	11.81	5
	7	9.1[†]	MCW0092-ADL0169	29	7.75	−2.30	4
	Z	6.3[†]	LEI0229	36	8.72	–	2
ESW	1b	9.9[†]	LEI0088-MCW0200	27	0.00	0.21	4
	4	11.6[†]	LEI0125-LEI0076	41	0.15	0.20	5
Lightness	6	9.3[†]	LEI0192	0	1.18	−1.17	4
	11	8.6[†]	LEI0072-LEI0214	19	−1.16	3.19	10
Redness	6	14.7[†]	LEI0192	0	−1.00	0.90	6
	11	16.9*	LEI0072-LEI0214	19	0.84	−2.56	19
Yellowness	6	10.9[†]	LEI0192	0	−1.51	1.02	4
	11	11.1[†]	LEI0072-LEI0214	19	0.97	−3.74	13
EPR	1a	9.0[†]	LEI0174	54	4.17	3.60	4
AFE	Z	17.7*	ADL0201-MCW0241	28	7.03	–	6

[1]Position of QTL relative to the first marker in the set for this chromosome. The first markers were shown in Fig. 1.

[2]The additive effect obtained from the Rhode Island Red QTL allele is half the phenotypic difference between birds carrying two Rhode Island Red alleles and those with two White Leghorn alleles.

[3]The dominance effect is a deviation of phenotypes of heterozygous birds from the mean of the groups of homozygous birds.

BW, body weight at 239 days of age; EW, egg weight; SLE, short length of egg; LLE, long length of egg; ESS, egg shell strength; EST, egg shell thickness; ESW, egg shell weight; Lightness, luminance or lightness component; Redness, chromatic component from green to red; Yellowness, chromatic component from blue to yellow; EPR, egg production ratio (169–280 days of age); AFE, age at first egg.

LRS: [†]suggestive linkage, *significant linkage at $P < 0.05$; **highly significant linkage $P < 0.01$.

Fujinaka 2001; Sewalem *et al.* 2002; Kerje *et al.* 2003) and chromosome 2 (Tatsuda & Fujinaka 2001; Sewalem *et al.* 2002; Kerje *et al.* 2003). The original breeds of families analysed in the earlier studies differ from those used in this study. However no QTL on chromosomes 1 and 2 were identified, either in this report or that by Tsuiskula-Haavisto *et al.* (2002). This discrepancy may be due to the character of the intercross between WL and RIR.

The QTL for EW was identified at a similar position on chromosome 4, compared with a previous study (Tsuiskula-Haavisto *et al.* 2002). Moreover, the additive and dominance effects were analogous. In this study, QTL for SLE and EW were assigned similar positions on chromosome 4. The phenotypic correlation between EW and SLE is 0.90. The greater weight of individual eggs is associated with an increase in egg width (Hocking *et al.* 2003). These results indicate that QTL for EW and SLE may be the same and that

the length of SLE is proportional to EW. The phenotypic correlation between EW and LLE was as high as 0.71, but only 0.44 between SLE and LLE. The QTL suggestively linked to LLE was 33.6 cM from the position of the QTL for EW on chromosome 4.

On chromosome 4, QTL for BW and EW were assigned to positions which were 12 cM on either side of *MCW0122*. The phenotypic correlation between BW and EW was 0.44 low, despite their nearness. However, BW has the potential to correlate with EW genetically, because the genetic correlation between BW and EW was 0.63 at 6 weeks of age (Koerhuis & McKay 1996), 0.31 at sexual maturity (Chatterjee *et al.* 2000) and 0.47 at 497 days (Poggenpoel *et al.* 1996), suggesting the QTL for BW may be located close to QTL for EW.

The suggestive QTL for ESS was assigned on the Z chromosome, and its additive effect was positive. The QTL

position of ESS on the Z chromosome is consistent with a previous report (Tsuiskula-Haavisto *et al.* 2002). But the directions of the additive effect of those two QTL differed, probably because the WL line used in this study was selected for reduced ESS. The physiological state for ESS control was difficult to assess from the data obtained in this study. The suggestive QTL for EST was detected 11 cM beyond that for ESS on the Z chromosome. Suggestive QTL for ESS and EST were detected at the same position on chromosome 1b, and at slightly different positions on chromosome 7. The phenotypic correlation between ESS and EST was as high as 0.82. QTL on chromosomes 1b and 4 were suggestively linked to ESS, EST and ESW, except that EST was not associated with QTL on chromosome 4. The correlation coefficients between ESS and ESW, and between EST and ESW were 0.64 and 0.78, respectively. The QTL positions for ESS and EST were similar, but slightly different from that for ESW. These QTL on chromosomes 1b and 4 have a large dominance effect and small additive effect, and would therefore be difficult to use for MAS.

A significant QTL for redness was detected on chromosome 11 at the same position as suggestive QTL for lightness and yellowness. Other suggestive QTL for redness, lightness and yellowness were detected at the same position on chromosome 6. The additive effect of QTL on chromosome 6 was positive for lightness, and negative for redness and yellowness. The additive effects of QTL on chromosome 11 were positive for redness and yellowness, and negative for lightness. QTL for egg shell colour have been reported on chromosomes 4 (Wardecka *et al.* 2002) and 5 (Wardecka *et al.* 2003) but we could not detect these in our study. Data from these two reports by Wardecka differed from our results. It is suggested that the different methods used for measurement by our group and that of Wardecka may account for the inconsistent results. The absolute values of phenotypic correlation among redness, lightness and yellowness were as high as 0.85–0.92. It seems that these three traits measured the amount of the same materials because the main of pigment of egg shell colour which is protoporphyrin, is a major component of the brown egg shell colour (Helbacka & Swanson 1958). Therefore the QTL of the three egg shell colour traits would be assigned the same position.

Significant QTL for AFE was detected on the Z chromosome close to the QTL reported previously (Tsuiskula-Haavisto *et al.* 2002). The additive effect observed this study was more significant than that discussed earlier. This information on QTL for AFE would facilitate selection, as the egg production trait cannot be measured in immature females and males.

Acknowledgements

References

ArkDB URL (2001) http://www.thearkdb.org/, Roslin Institute, UK.

van der Beek S. & van Arendonk J.A.M. (1996) Marker-assisted selection in an outbred poultry breeding nucleus. *Animal Science (Pencaitland)* **62**, 171–80.

Chatterjee R.N., Misra B.S. & Singh H.N. (2000) Time trends in estimates of genetic parameters in a White Leghorn population subjected to long-term selection. *Indian Journal of Animal Sciences* **70**, 184–7.

Churchill G.A. & Doerge R.W. (1994) Empirical threshold values for quantitative trait mapping. *Genetics* **138**, 963–71.

Groenen M.A.M., Crooijmans R.P.M.A., Veenendaal T., Van Kaam J.B.C.H.M., Wereijken A.L.J., Van Arendonk J.A.M. & Van der Poel J.J. (1997) QTL mapping in chicken using a three generation full sib family structure of an extreme broiler × broiler cross. *Animal Biotechnology* **8**, 41–6.

Groenen M.A.M., Cheng H.H., Bumstead N. *et al.* (2000) A consensus linkage map of the chicken genome. *Genome Research* **10**, 137–47.

Haley C.S. & Knott S.A. (1992) A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. *Heredity* **69**, 315–24.

Hamilton R.M.G., Hollands K.G., Voisey P.W. & Grunder A.A. (1979) Relationship between egg shell quality and shell breakage and factors that affect shell breakage in the field – a review. *World's Poultry Science Journal* **35**, 177–90.

Helbacka N.V. & Swanson M.H. (1958) Studies on blood and meat spots in the hen's egg. 2. some chemical and histological characteristics of blood and meat spots. *Poultry Science* **37**, 877–85.

Hocking P.M., Bain M., Channing C.E., Fleming R. & Wilson S. (2003) Genetic variation for egg production, egg quality and bone strength in selected and traditional breeds of laying fowl. *British Poultry Science* **44**, 365–73.

Hunton P. (1962) Genetics of egg shell color in a light sussex flock. *British Poultry Science* **3**, 189–93.

van Kaam J.B.C.H.M., van Arendonk J.A.M., Groenen M.A.M., Bovenhuis H., Vereijken A.L.J., Crooijmans R.P.M.A., van der Poel J.J. & Veenendaal A. (1998) Whole genome scan for quantitative trait loci affecting body weight in chickens using a three generation design. *Livestock Production Science* **54**, 133–50.

van Kaam J.B.C.H.M., Groenen M.A.M., Bovenhuis H., Veenendaal A., Vereijken A.L.J. & van Arendonk J.A.M. (1999) Whole genome scan in chickens for quantitative trait loci affecting growth and feed efficiency. *Poultry Science* **78**, 15–23.

Kerje S., Carlborg O., Jacobsson L., Schutz K., Hartmann C., Jensen P. & Andersson L. (2003) The twofold difference in adult size between the red junglefowl and White Leghorn chickens is largely explained by a limited number of QTLs. *Animal Genetics* **34**, 264–74.

Koerhuis A.N.M. & McKay J.C. (1996) Restricted maximum likelihood estimation of genetic parameters for egg production traits in relation to juvenile body weight in broiler chickens. *Livestock Production Science* **46**, 117–27.

Lee E.J., Yoshizawa K., Mannen H., Kikuchi H., Kikuchi T., Mizutani M. & Tsuji S. (2002) Localization of the muscular dystrophy AM locus

using a chicken linkage map constructed with the Kobe University resource family. *Animal Genetics* **33**, 42–8.

Manly K.F. & Cudmore R.H. Jr (2001) Map Manager QTX, cross-platform software for genetic mapping. *Mammalian Gemome* **12**, 930–2.

Martinez O. & Curnow R.N. (1992) Estimating the locations and the size of the effects of quantitative trait loci using flanking markers. *Theoretical and Applied Genetics* **85**, 480–8.

Meuwissen T.H.E. & Goddard M.E. (1996) The use of marker haplotypes in animal breeding schemes. *Genetics Selection Evolution (Paris)* **28**, 161–76.

Nirasawa K., Takahashi H., Takeda H., Furukawa T., Takeda T. & Nagamine Y. (1998) Restricted maximum likelihood estimates of genetic parameters and genetic trends of chickens divergently selected for eggshell strength. *Journal of Animal Breeding & Genetics-Zeitschrift fur Tierzuchtung und Zuchtungsbiologie* **115**, 375–81.

Poggenpoel D.G., Ferreira G.F., Hayes J.P. & Du Preez J.J. (1996) Response to long-term selection for egg production in laying hens. *British Poultry Science* **37**, 743–56.

Sewalem A., Morrice D.M., Law A., Windsor D., Haley C.S., Ikeobi C.O.N., Burt D.W. & Hocking P.M. (2002) Mapping of quantitative trait loci for body weight at three, six, and nine weeks of age in a broiler layer cross. *Poultry Science* **81**, 1775–81.

Tatsuda K. & Fujinaka K. (2001) Genetic mapping of the QTL affecting body weight in chickens using a F2 family. *British Poultry Science* **42**, 333–7.

Tatsuda K., Fujinaka K. & Yamasaki T. (2000) Genetic mapping of a body weight trait in chicken. *Animal Science Journal* **71**, 130–6.

Tsuiskula-Haavisto M., Honkatukia M., Vilkki J., de Koning D.-J., Schulman N.F. & Maki-Tanila A. (2002) Mapping of quantitative trait loci affecting quality and production trait in egg layers. *Poultry Science* **81**, 919–27.

US Poultry Genome Project (2001) http://poultry.mph.msu.edu/, Michigan State University, East Lansing, MI, USA.

Wardecka B., Olszewski R., Jaszczk K., Zieba G., Pierzchala M. & Wicinska K. (2002) Relationship between microsatellite marker alleles on chromosomes 1–5 originating from the Rhode Island Red and Green-legged Partrigenous breeds and egg production and quality traits in F2 mapping population. *Journal of Applied Genetics* **43**, 319–29.

Wardecka B., Olszewski R., Jaszczk K., Zieba G. & Pierzchala M. (2003) Preliminary mapping of QTLs affecting egg quality on chromosome 1–5 in chickens. *Czech Journal of Animal Science* **48**, 97–105.

Yasukouchi Y. (1998) A dense genetic map of the silkworm, *Bombyx mori*, covering all chromosomes based on 1018 molecular markers. *Genetics* **150**, 1513–25.

Zeng Z.-B. (1993) Theoretical basis for separation of multiple linked gene effects in mapping quantitative trait loci. *Proceeding of the National Academy of Sciences of the United States of America* **90**, 10972–6.

Zeng Z.-B. (1994) Precision mapping of quantitative trait loci. *Genetics* **136**, 1457–68.